CHEENEETNUKIIDAE, A NEW MIDDLE DEVONIAN MURCHISONIOID GASTROPOD FAMILY, INCLUDING THE NEW GENERA *CHEENEETNUKIA* AND *ULUNGARATOCONCHA* BASED ON REPRESENTATIVES FROM ALASKA AND AUSTRALIA

ROBERT B. BLODGETT AND ALEX G. COOK

Blodgett, R.B. & Cook, A.G. 2002 5 31: Cheeneetnukiidae, a new Middle Devonian murchisonioid gastropod family, including the new genera *Cheeneetnukia* and *Ulungaratoconcha* based on representatives from Alaska and Australia. *Memoirs of the Queensland Museum* **48**(1): 17-28. Brisbane. ISSN 0079-8835.

Two new genera of murchisonioid gastropods, *Cheeneetnukia* and *Ulungaratoconcha*, are established from the Middle Devonian (Eifelian and Givetian) strata of the Old World Realm and are placed in Cheeneetnukiidae fam. nov. belonging to Murchisonioidea. Cheeneetnukiidae represent a distinctive group of Middle Devonian murchisonioids characterised by a squared-off (rectangular) whorl profile, a flattened vertical outer whorl surface with a broad, centrally situated selenizone which is bounded above and below by strong angulations, often in the form of flange-like projections. Strongly ornate (nodose or spinose) forms are common amongst the younger Givetian representatives of the family. The family underwent an explosive adaptive radiation of intricate and highly decorated forms that are restricted to the Middle Devonian (Eifelian and Givetian). The family is characteristic for warm tropical seaways of the Middle Devonian, and its representatives are known from Germany, various accreted Alaskan terranes (Farewell, Alexander and Arctic Alaska), northeastern Australia, Malaysia and southern China. Three new species are here described:1) the type species of *Cheeneetnukia*, *C. frydai* from the Eifelian of Alaska, known from both the Cheeneetnuk Limestone of west-central Alaska (Nixon Fork subterrane of the Farewell terrane) and the Wadleigh Limestone from southeastern Alaska (Alexander terrane); 2) *C. australis* from the uppermost Dosey Limestone (early Givetian) of north Queensland, Australia; and 3) the type species of *Ulungaratoconcha*, *U. heidelbergeri* from Eifelian strata of the Ulungarat Formation (Member A), northeastern Brooks Range, northeastern Alaska (Arctic Alaska terrane). ❐ *Devonian, Alaska, Australia, Gastropoda, Cheeneetnukiidae.*

Robert B. Blodgett , Department of Zoology, Oregon State University, Corvallis, Oregon 97331, U.S.A.(e-mail: blodgetr@bcc.orst.edu); and Alex G. Cook, Queensland Museum, PO Box 3300 South Brisbane 4101, Australia; *received 1 April 2002.*

Murchisonioid gastropods underwent significant speciation during the Middle Devonian resulting in a plexus of unusual medium to large-sized, often nodose or spinose forms (Andree, 1928; Grüneberg, 1927; Paeckelmann, 1922). This radiation was also mentioned by Knight et al. (1960: I291) who in reference to *Murchisonia* stated: 'In Middle Devonian close relatives of the type species display a burst of forms with elaborate, in part bizarre, shapes and ornament quite incongruous with usual conservatism shown by genus'. Such bizarre murchisonioids characterise typical Old World Realm Middle Devonian (all Givetian in age) faunas in Europe (D'Archaic & DeVerneuil, 1842; Goldfuss, 1841-1844; Sandberger & Sandberger, 1850-1856; Whidborne, 1889-1892; Lotz, 1900; Kirchner, 1915; Heidelberger, 2001), southern China (Mansuy, 1912; Cook, pers. obs.) and to a lesser extent western Canada (Whiteaves, 1892) and Australia (Cook & Camilleri, 1997). This unusually ornate group of murchisonioid gastropods is characterised by a distinctive, 'squared-off' rectangular whorl profile which clearly distinguishes it, and for which we erect Cheeneetnukiidae fam. nov. In the family, we establish *Cheeneentukia* gen. nov. from S Alaska (Farewell and Alexander terranes) and NE Australia, and *Ulungaratoconcha* gen. nov. based on a NE Alaskan species, but which also includes many species recognised primarily in Europe. Both new genera are associated with the early phases of explosive adaptive radiation shown by the family. *Ulungaratoconcha* gen. nov. has been referred to in an earlier paper (Popov et al., 1994: 1214) simply as a 'new genus of murchisoniid gastropod'. In that same paper, devoted to the description of a new inarticulate brachiopod, this new gastropod genus was noted as occurring in the Ulungarat Formation of

Anderson (1991) of the Demarcation Point A-4 quadrangle, NE Brooks Range (Arctic Alaska terrane).

As noted above, *Cheeneetnukia* gen. nov. is also recognised in the uppermost Dosey Limestone (early Givetian) of N Queensland. Reconstructions of Scotese & McKerrow (1989) and Metcalfe (1996) show eastern Gondwana representing the farthest extent of the Old World Realm, with a significant distance across a proto-Pacific ocean (commonly called Panthalassa) to the Americas. The distribution of this new taxon is anomalous and suggests biogeographic pathways linking the Alaskan terranes (or blocks) to eastern Gondwana during the Middle Devonian. On the basis of Devonian biogeographic evidence (primarily brachiopods), as well as supporting evidence from other time intervals in the Early and Middle Palaeozoic, it has been recently suggested that the major Alaskan terranes with significant Devonian faunas such as the Farewell, Livengood, Arctic Alaska, and Alexander terranes, represent continental margin blocks which have been rifted apart from the Siberian palaeocontinent during Devonian time (Blodgett & Brease, 1997; Blodgett, 1997; Blodgett & Boucot, 1999; Garcia-Alcalde & Blodgett, 2001; Blodgett et al., in press).

SYSTEMATIC PALAEONTOLOGY

Type specimens of *Cheeneetnukia frydai* sp. nov. and *Ulungaratoconcha heidelbergeri* sp. nov. are deposited in the University of Alaska Museum (UAM) at Fairbanks, Alaska, and those of *C. australis* sp. nov. are deposited in the Queensland Museum (QMF), Brisbane.

Suborder MURCHISONIINA Cox & Knight, 1960
Superfamily MURCHISONIOIDEA Koken, 1896
Family MURCHISONIIDAE Koken, 1896

REMARKS. The Murchisoniidae (sensu Knight et al., 1960) is recognised as polyphyletic, as shown by recent protoconch studies of some of its constituent genera. The protoconch of the type species of *Murchisonia*, *M. bilineata* (Dechen, 1832), as well as those of closely related Middle Devonian species remains unknown; however, Frýda & Manda (1997) and Frýda (1999a) demonstrated an archaeogastropod type protoconch in a number of Early Devonian species of *Murchisonia* from the Prague Basin. In contrast, Nützel & Bandel (2000) demonstrated a caenogastropod type protoconch in members of their newly established Goniasmidae, including *Goniasma*, *Stegocoelia*, and *Cerithioides*, which they transferred from the Murchisoniidae to the order Cerithimorpha of the subclass Caenogastropoda.

We regard all subgenera of *Murchisonia* recognised by Knight et al. (1960), as well as the subsequently established *Murchisonia* (*Ostioma*) Tassell, 1980, to be independent taxa worthy of generic rank within the Murchisoniidae. *Murchisonia* should be restricted to those species that are closely allied with the type species, *M. bilineata* (Dechen, 1832) from the Middle Devonian (Givetian) of Germany. *Murchisonia* has for over a century and a half served as 'catch-all' for a vast array of species characterised only in being relatively high-spired and possessing a selenizone. In light of the now obvious polyphyletic origin of many of its members, based on protoconch studies and the great diversity of teleoconch morphologies, we believe both *Murchisonia* and the Murchisoniidae are long overdue for intensive revision.

Family CHEENEETNUKIIDAE fam. nov.

DIAGNOSIS. Medium- to large-sized; whorl profile distinctly squared-off (rectangular), with a flat to moderately inclined upper whorl surface, below which is a vertical, flattened outer whorl surface bearing a broad, centrally situated selenizone; upper and lower boundaries of the outer whorl surface marked by strong angulations, often projecting abaxially as a flange; protuberances, spines, and nodes are commonly well developed.

REMARKS. The Cheeneetnukiidae is easily distinguished within the Murchisonioidea by its characteristically squared-off (rectangular) whorl profile. In other murchisonioids, the whorl profile is typically V-shaped or rounded. The type species of *Murchisonia*, *M. bilineata* (Dechen, 1832) from the Givetian of Germany, closely resembles members of the Cheeneetnukiidae but lacks the characteristic whorl profile of the new family. Based on the gross similarity of the Cheeneetnukiidae to the Murchisoniidae it is likely that both families are closely related and belong to the Archaeogastropoda, but knowledge of the protoconch is needed to corroborate this supposition. Cheencetukiidae and Murchisoniidae could share a common ancestor that gave rise to both highly diverse Devonian groups. Alternatively the presence of members of the Caenogastropoda and Heterobranchia in Devonian strata (Frýda &

Blodgett 2001, Frýda 2001) as well as shell homplasy in Devonian gastropods (Frýda, 1999b) complicate this interpretation. The adaptive significance of the distinctive whorl profile is presently unknown.

COMPOSITION. Members of the new family embrace the bizarre array of strange-shaped and ornate Middle Devonian murchisonioids that has previously been noted by earlier workers (Knight et al., 1960: 1291; Paeckelmann, 1922; Grüneberg, 1927; Andree, 1928). It is obvious that an explosive adaptive radiation occurred among members of this group, known only from Middle Devonian strata of the Old World Realm (Germany, Alaska, Australia, southern China). We distinguish two new genera within the family, *Cheeneetnukia* and *Ulungaratoconcha*, but believe that other species (nearly all assigned earlier to *Murchisonia*) within this plexus of distinctive murchisonioids will be assigned to separate genera pending further study.

Cheeneetnukia gen. nov.

TYPE SPECIES. *Cheeneetnukia frydai* gen. et sp. nov. from the upper Cheeneetnuk and Wadleigh Limestones, Alaska.

ETYMOLOGY. After the Cheeneetnuk Limestone.

DIAGNOSIS. Large, high-spired gradate, with a broad, flat subsutural ramp terminateing at a projecting flange-like upper carina, the latter forming the shell periphery. Mid-whorl section vertical to weakly inclined inward, with a broad, flat selenizone bounded by two fine, weakly raised spiral threads. A lower, weaker carina forming the boundary between the mid-whorl section and the base. Succeeding whorls joining previous whorls at or just below lower carina. Base with narrow, but relatively deep umbilicus.

COMPARISON. The unusual whorl profile of *Cheeneetnukia* with its two strong angulations, the upper of which forms a prominent projecting flange-like carina and delimits a nearly flat, vertical outer whorl face, separates this genus from known murchisonioid genera. It is distinguished in its broad, gradate (step-like) shell from the only other genus assigned to the family, *Ulungaratoconcha* gen. nov., which possesses a narrowly acute shell.

COMPOSITION. *C. frydai* sp. nov.; *C. australis* sp. nov.

A third undescribed species may be present in the Givetian Ertang Formation of Guangxi, China, but it is currently under review (Cook, pers. obs.). Another undescribed species, *Murchisonia* sp. C (Suntharalingam, 1968, fig. 12) from the Givetian Thye On beds near Kampar, Perak, Malaysia also appears to belong to *Cheeneetnukia*.

In addition, the following ornate Givetian species from Germany and England show some striking resemblance to *Cheeneetnukia*, notably in the broad spired, gradate form of the shell, and may prove to be closely related or descended from *Cheeneetnukia*. These include (using original author designation):
Murchisonia spinosa Phillips, 1841; Givetian of England and Germany.
Murchisonia seminodosa Grüneberg, 1927; Givetian of Germany.
Murchisonia coronata var. *turboides* Winterfeld, 1894; Givetian of Germany

Cheeneetnukia frydai sp. nov.
(Figs 1-3)

TYPES. Holotype, UAM2639; paratypes,A-I, UAM 2640-2649. The types are from locality 83RI38 in the McGrath A-5 quadrangle (Cheeneetnuk Limestone), west-central Alaska. A non-type specimen (UAM 2649) is also illustrated from USGS locality M1299-SD in the Craig D-4 quadrangle (Wadleigh Limestone), SE Alaska.

ETYMOLOGY. For Dr Jiri Frýda.

DIAGNOSIS. Upper angulation extremely strong, protruding, flange-like.

DESCRIPTION. Large, gradate, broad, high-spired shell; whorls up to 8 in teleoconch, protoconch not preserved; whorl profile distinctly 'squared-off' (rectangular) with two prominent angulations, one formed by strongly projecting carina situated at upper/outer whorl surface junction that forms the shell periphery, the other formed by less strongly projecting carina situated at outer/basal whorl face junction; sutures of variable strength, ranging from weak to strongly impressed, situated immediately beneath carina forming lower angulation; upper whorl face broad, commonly flat or rarely concave, horizontal or weakly inclined downward abaxially; outer whorl face flat to weakly concave, vertical to subvertical (slightly inclined inward basally); selenizone relatively broad, its surface smooth, slightly recessed, bearing weak lunulae, bordered by two fine spiral threads; base moderately convex, minutely phaneromphalous (but deep) in fully adult shells, cryptomphalous in juvenile specimens;

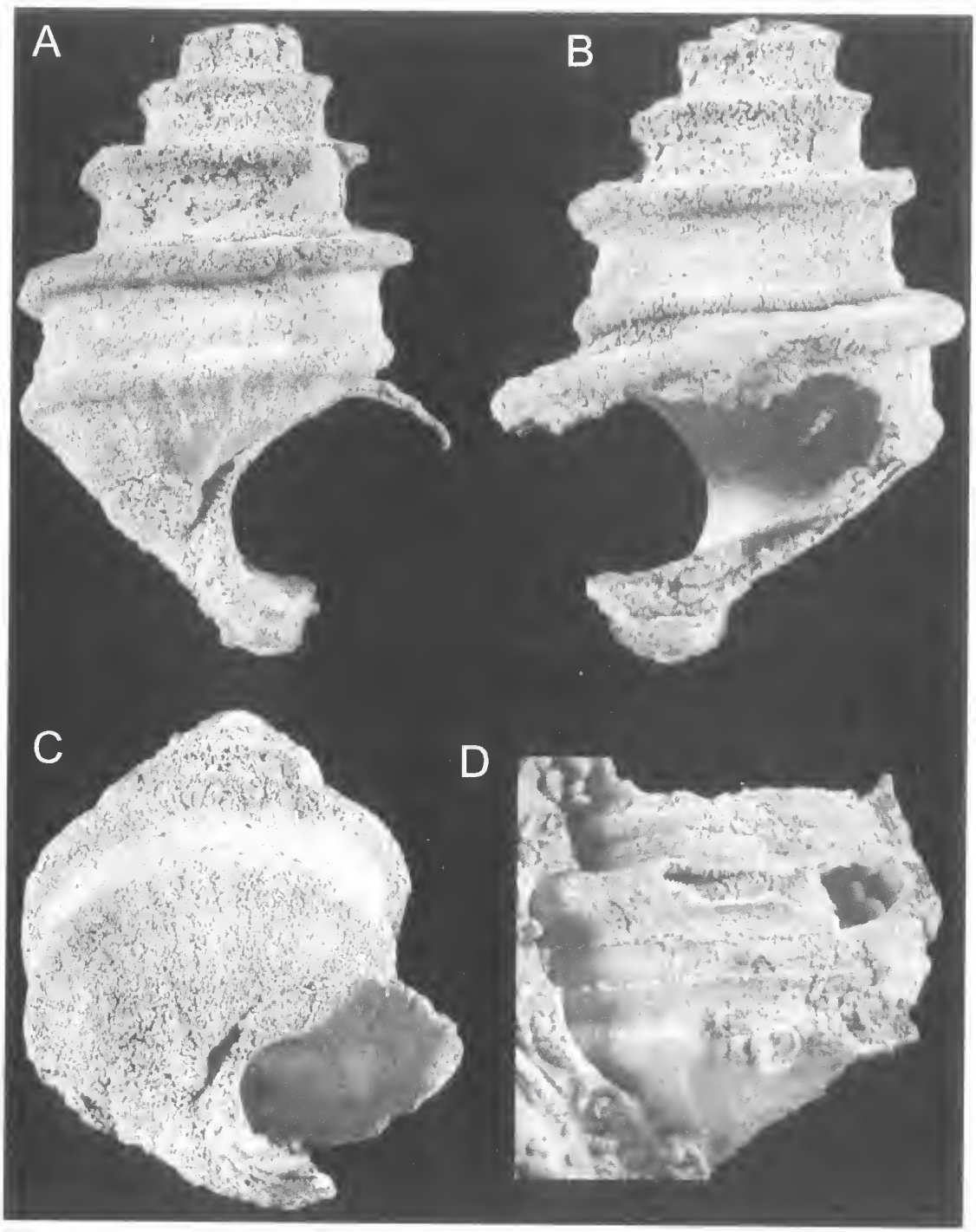

FIG. 1. A-D, *Cheeneetnukia frydai* gen. et sp. nov. A-C, Holotype UAM 2639, × 1.5. A, apertural view; B, abapertural view; C, oblique basal view. D, Paratype A UAM 2640, × 2, side view of shell fragment preserving penultimate and final whorls (note well developed centrally situated selenizone). Both specimens are from locality 79RB8 (USGS locality 10061-SD), McGrath A-5 quadrangle, west-central Alaska.

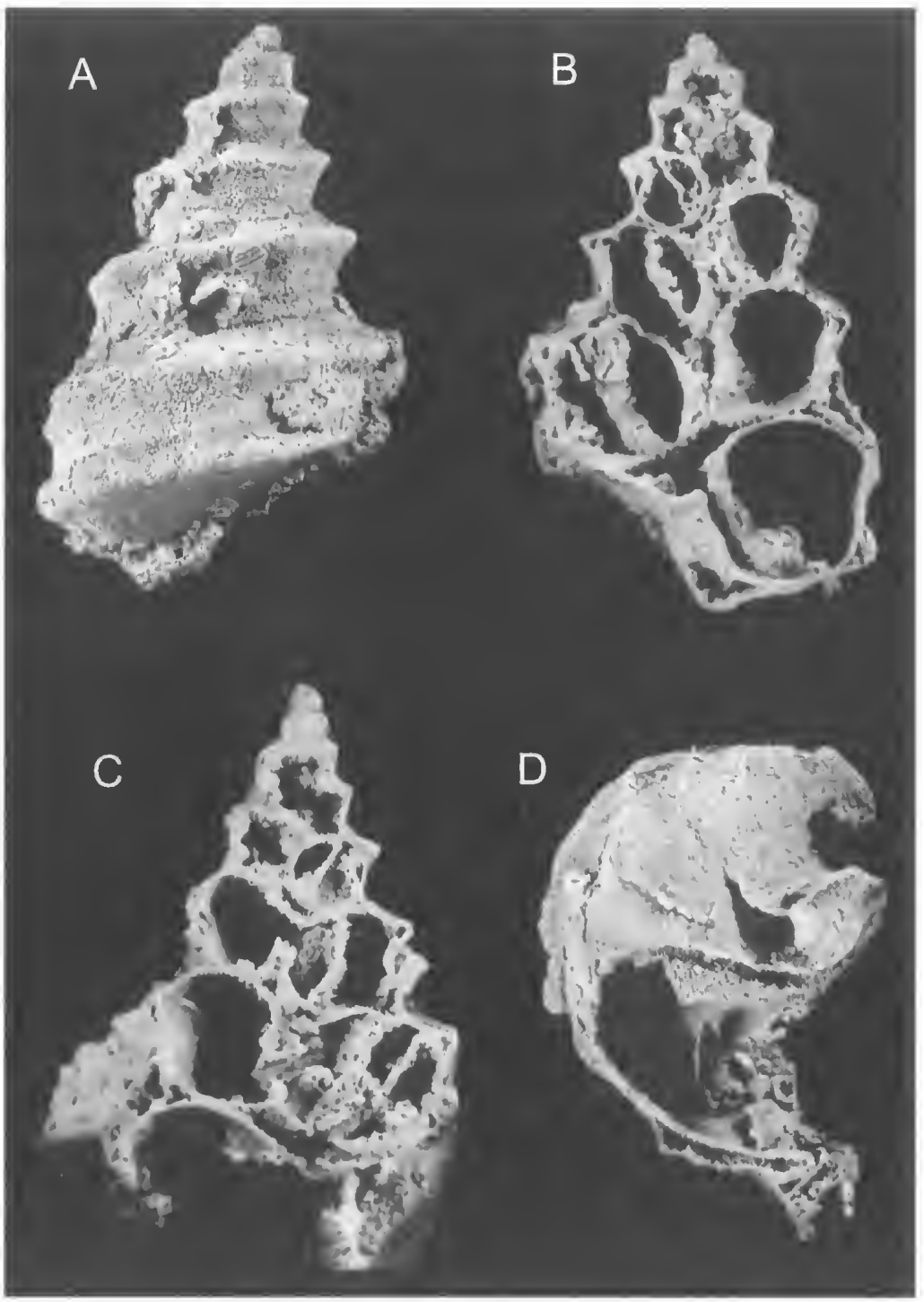

FIG. 2. A-D, *Cheeneetnukia frydai* gen. et sp. nov. A-B, Paratype B UAM 2641, × 2. A, abapertural view; B, natural longitudinal section through same specimen. C, Paratype C UAM 2642, × 2, longitudinal (natural) section (note distinctive external whorl typical for the Cheeneetnukiidae). D, Paratype D UAM 2643, × 1.5, basal view. All specimens are from locality 79RB8 (USGS locality 10061-SD), McGrath A-5 quadrangle, west-central Alaska.

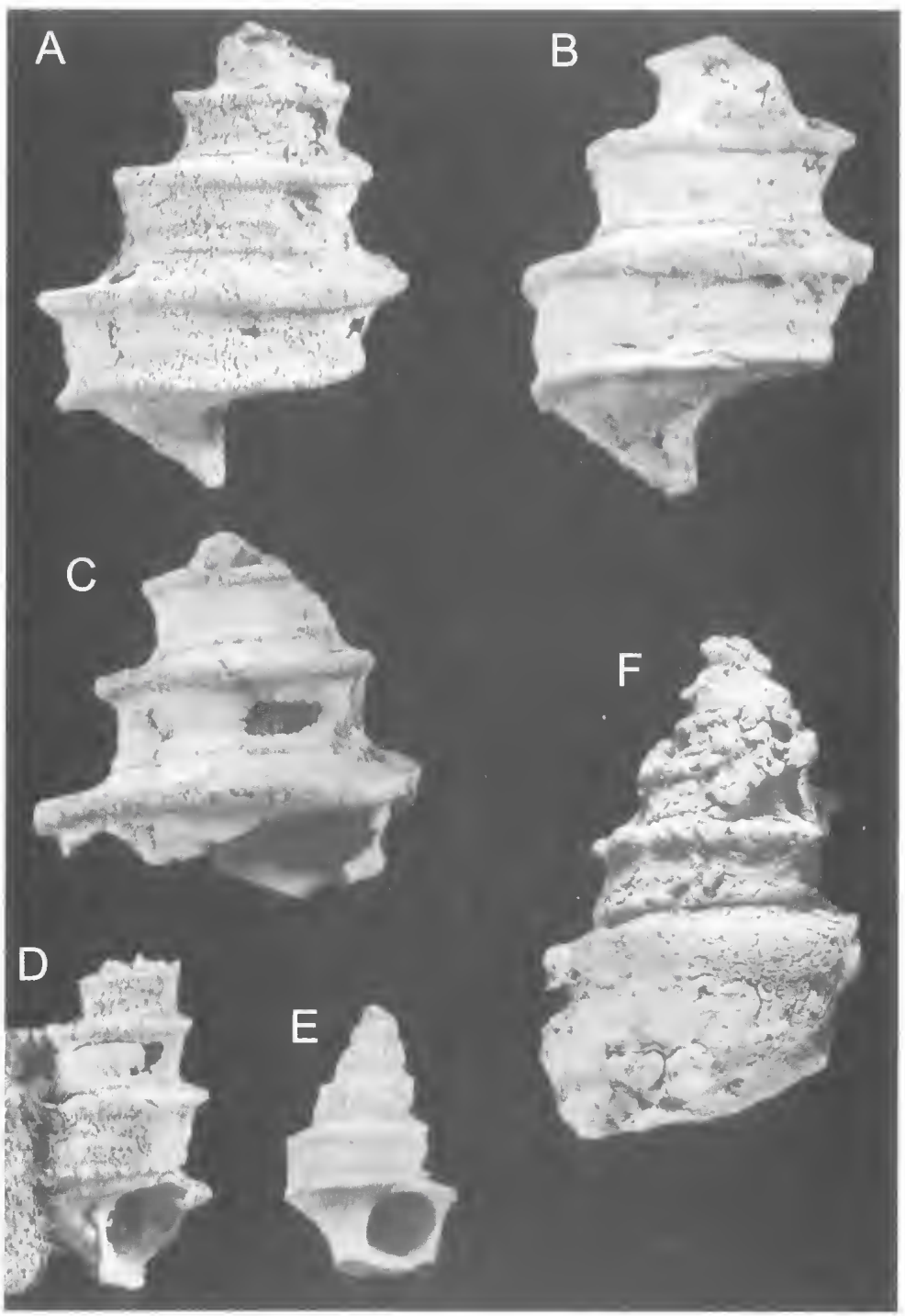

FIG. 3. A-F, *Cheeneetnukia frydai* gen. et sp. nov. A, Paratype E UAM 2644, × 2, apertural view. B, Paratype F UAM 2645, × 2, apertural view. C, Paratype G UAM 2646, × 2, side view of shell fragment. D, Paratype H, UAM 2647, × 2, apertural view. E, Paratype I, UAM 2648, × 3, apertural view. F, UAM 2649, x 1.5, side view of coarsely preserved silicified specimen. A-E from locality 79RB8 (USGS locality 10061-SD), McGrath A-5 quadrangle, west-central Alaska, F from USGS locality M1299-SD, Craig D-4 quadrangle, southeast Alaska.

columellar lip thin, arcuate, recurved; outer lip unknown; growth lines typically not preserved, but visible on a few upper whorl surfaces where they are weakly prosocline (nearly orthocline).

REMARKS. The largest complete specimen in the collection is the holotype with the following dimensions: height (incomplete), 58.0mm; width (incomplete), 40.0mm. As noted above, the depth of the umbilicus is variable, in adult specimens it is minutely phaneromphalous, but width is variable (compare Figs 1C and 2D), in juvenile specimens the base of the shell is typically cryptomphalous. The 'squared-off' (rectangular) whorl profile is clearly shown in Fig. 2B, C. Several specimens show a weak development of nodes along the flange-like carina that forms the upper angulation, weakly anticipating the more strongly nodose character of many Givetian members of the Cheeneetnukiidae.

COMPARISON. This species differs from *Cheeneetnukia australis* in having a more strongly developed and protruding flange-like upper angulation.

OCCURRENCE. This species is especially abundant and one of the most abundant at locality 79RB8 (>128 specimens) in the upper part (early Eifelian) of the Cheenectnuk Limestone in the McGrath A-5 quadrangle, west-central Alaska (Nixon Fork subterrane of the Farewell terrane). The species is also present in lesser abundance in nearby, stratigraphically higher locality 79RB9. Both horizons are approximately 3 m thick and located along the type section traverse; the top of older horizon and the top of the younger horizon are 101m and 82m below the top of the Cheeneetnuk Limestone, respectively. Each locality is essentially the same on the 1:63,360 scale McGrath A-5 quadrangle map (Rigby & Blodgett, 1983, fig. 1; Blodgett & Rohr, 1989: fig. 2). The age of these two localities is probably late early to middle Eifelian, based on the co-occurrence and range overlap of the conodont *Polygnathus costatus costatus* (ident. N.M. Savage in Blodgett & Gilbert, 1983) and the ammonoid *Pinacites jugleri* (House & Blodgett, 1982). In addition, this new gastropod species is also recognised from Eifelian strata of the Wadleigh Limestone in the Craig D-4 quadrangle, SE Alaska (Alexander terrane). It is present there in a collection (field number 68AEs596; =USGS locality M1299-SD) made by J. Evans of the U.S. Geological Survey in 1988; specimens from there being coarsely silicified. The locality is situated on the shoreline of a small islet in the NW¼, NE¼, section 34, T70S, R79E, Craig D-4 quadrangle.

Cheeneetnukia australis sp. nov.
(Fig. 4A,B)

murchisoniid indet. Cook & Camilleri 1997: 71, fig. 4A-B.

TYPES. Holotype QMF33100 (Cook & Camilleri, 1997, fig. 4A); Paratypes QMF33097 and 34529 (Cook & Camilleri, 1997: fig. 4B), all from Queensland Museum Locality 1019.

ETYMOLOGY. Latin, *australis*, southern.

DIAGNOSIS. Upper angulation markedly reduced, weakly protruding.

DESCRIPTION. Medium-sized, moderately high-spired, turbiniform gradate shell up to 28mm high and 20mm wide, with an apical angle of c. 30°. Upper whorl surface with prominent sutural ramp sloping very gently to peripheral rounded keel. Midwhorl surface wide and vertical, with selenizone bordered by 2 weak threads. Lower whorl face rounded, but poorly known in the material. Suture slightly impressed, situated at lower part of midwhorl surface. Base unknown. Collabral growth lines, fine, numerous, closely spaced, prosocline on sutural ramp and above selenizone, opisthocline below selenizone. [original description of Cook & Camilleri (1997: 71)].

COMPARISON. This species differs from the type species, *C. frydai*, primarily in having a less prominently protruding upper angulation and in having much stronger spiral threads bordering the selenizone.

OCCURRENCE. Represented by three specimens from the uppermost Dosey Limestone (early Givetian, *ensensis* - lower *varcus* CZ), Broken River Province, north Queensland. This species differs from *C. frydai* in having a much less protruding flange-like upper angulation, but nevertheless is congeneric in every other respect.

Ulungaratoconcha gen. nov.

TYPE SPECIES. *Ulungaratoconcha heidelbergeri* gen. et sp. nov. from the Middle Devonian (Eifelian) strata of the Ulungarat Formation (Anderson, 1991), Alaska.

ETYMOLOGY. *Ungularat*, for the Ulungarat Formation and *concha* Latin for shell.

DIAGNOSIS. Narrowly acute, turbiniform, high-spired shell with flat to gently inclined, relatively narrow ramp-like upper whorl face and

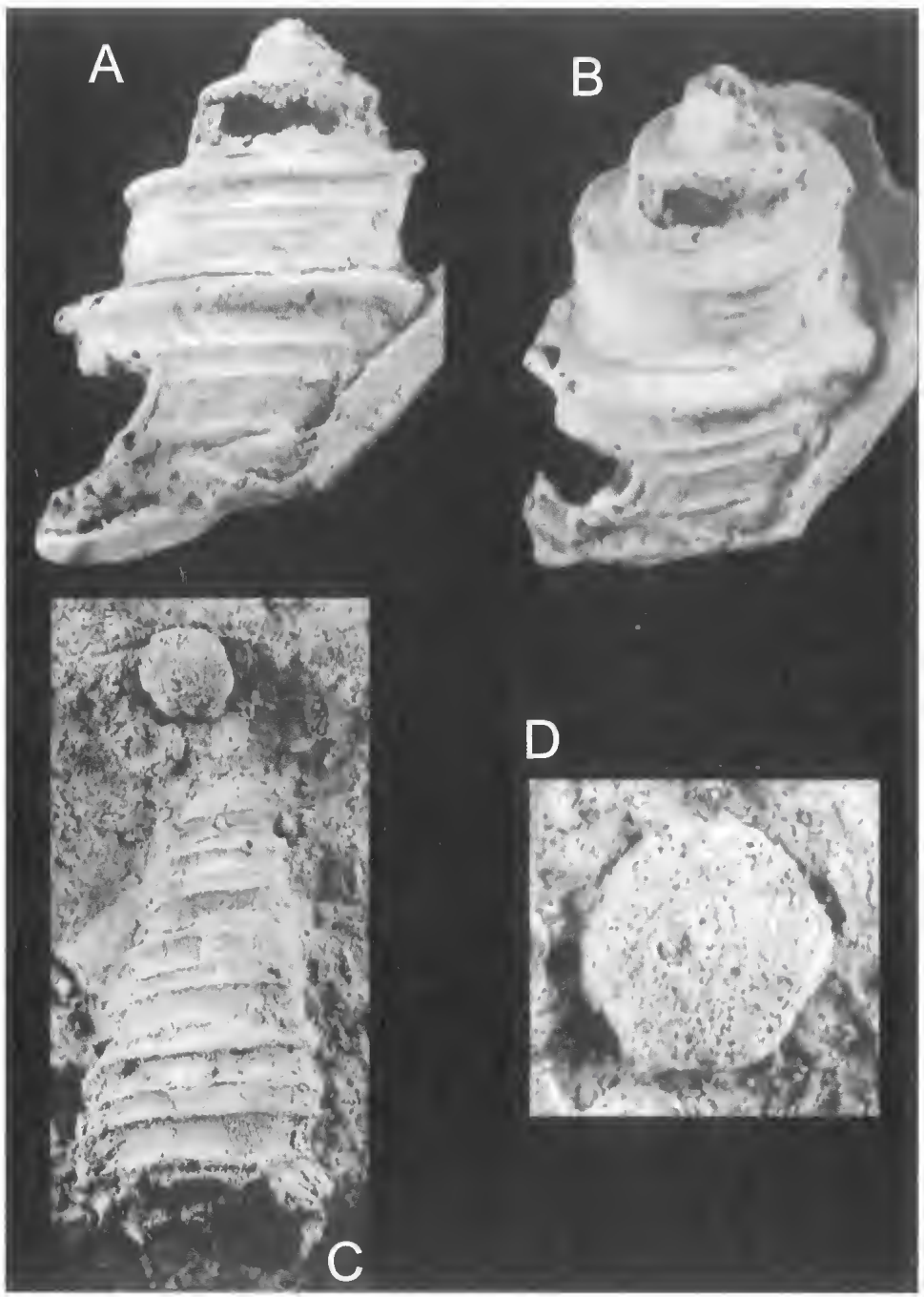

FIG. 4. A-B, *Cheeneetnukia australis* gen. et sp. nov. Latex repliea of Holotype, QMF33100, × 2. A, side view; B, oblique side view. C, *Ulungaratoconcha heidelbergeri* gen. et sp. nov. Latex replica of Holotype, UAM 2650, × 3, side view. D, *Coelotrochium* sp., a ealcareous green alga (same speeimen above gastropod shown in C) eommonly found in Eifelian age shallow-water gastropod-dominated communities in Alaska's aeereted terranes (i.e. Farewell, Alexander, Livengood, and Aretic Alaska terranes), × 9. A-B is from the uppermost Dosey Limestone (early Givetian), north Queensland, and C-D are from the Ulungarat Formation in the Demareation D-4 quadrangle, northeast Brooks Range, northeast Alaska (North Slope subterrane of the Aretie Alaska terrane).

vertical outer whorl face with centrally situated selenizone; upper/outer angulation commonly produced into a strongly protruding flange-like ridge. Younger members (Givetian) may develop nodes or spines.

COMPARISON. *Ulungaratoconcha* gen. nov. shares the distinctive squared-off whorl profile and distinctive flange-like upper angulation also found in *Cheeneetnukia* gen. nov., but is easily distinguished from it by its narrowly acute spire, compared to the broad, gradate (step-like) shell form of the latter genus.

COMPOSITION. Species names are given after original author usage. Heidelberger (2001) provided excellent photographs of many of these species.

Ulungaratoconcha heidelbergeri gen. et sp. nov. (type species); Eifelian of Alaska.
Murchisonia coronata D'Archiac & DeVerneuil, 1842; Givetian of Germany.
Murchisonia archiaci var. *intermediacoronata* Andree, 1928; Givetian of Germany.
Murchisonia bigranulosa D'Archiac & DeVerneuil, 1842; Givetian of Germany.
Murchisonia binodosa D'Archiac & DeVerneuil, 1842; Givetian of Germany.
Murchisonia intermedia D'Archiac & DeVerneuil, 1842; Givetian of Germany.
Murchisonia archiaci var. *coronataturbinata* Andree, 1928; Givetian of Germany.
Murchisonia archiaci var. nov. *bicoronata* Paeckelmann, 1922; Givetian of Germany.
Murchisonia hibernia Heidelberger, 2001; Givetian of Germany.
Murchisonia pseudobinodosa Heidelberger, 2001; Givetian of Germany.

Ulungaratoconcha heidelbergeri sp. nov.
(Fig. 4C)

MATERIAL. Holotype, UAM 2650.

ETYMOLOGY. For Karlheinz Heidelberger, husband and ardent field assistant of German Devonian gastropod worker Doris Heidelberger.

DIAGNOSIS. Spire highly acute, narrow; lacking nodes or spines.

DESCRIPTION. Medium-sized (16.8mm (incomplete) high; 9.3mm wide], acutely high-spired (pleural angle about 12°), turbiniform shell; whorls up to at least five; sutures weakly incised, situated immediately beneath projecting edge of lower angulation; protoconch and initial portion of shell unknown; upper whorl face formed by moderately inclined, narrow ramp, outer whorl face flattened, weakly convex, with relatively broad (occupying about 1/3 of whorl face), centrally located selenizone, the latter bordered by two strongly raised, sharp-edged spiral threads which project to form shell periphery, boundary between upper and outer whorl faces occupied by flange-like projecting upper angulation, lower boundary of outer whorl face formed by lower angulation which likewise bears a strongly projecting flange-like edge; growth lines prosocline (closely approaching orthocline) on upper whorl face, those on outer whorl face are evenly and more strongly inclined at approximately 60° from horizontal, being prosocline above and opisthocline below the selenizone; surface of selenizone flat, with no visible lunulae; base of shell unknown.

COMPARISON. This species, the oldest known representative of the genus, most closely resembles the Givetian *Murchisonia coronata* D'Archiac & DeVerneuil, 1842, and *M. intermediacoronata* Andree, 1928, but is distinguished from both in having a more narrowly acute spire. Its lack of nodes or spines distinguishes it from most of the other species provisionally placed in the genus.

OCCURRENCE. The single specimen was collected by Arlene V. Anderson (then a doctoral student at the University of Alaska Fairbanks). It is from the Ulungarat Formation (Anderson, 1991) exposed in the NE Brooks Range. The locality (field number 89A-126A_1) is within member A, the lowermost and only marine unit of the four members (Anderson, 1991, 1993). The collection which yielded this sample was derived from a 14m thick interval of chert arenite and siltstone with thin interbeds of mudstone that forms the base of her measured section 89A-118, situated at and just below the 6,000 foot contour elevation in the SW¼, NW¼, SE¼, section 16, T5S, R37E, Demarcation Point A-4 quadrangle (Anderson, 1993: 228). This interval comprises the lowermost in-place outcrop above a loose scree slope. This new gastropod species has previously been cited as representing a 'new genus of murchisoniid gastropod' (Popov et al, 1993: 1214; Blodgett et al., in press). The sandstone piece that yielded this specimen also contains the dasyclad alga *Coelotrochium* (Fig. 4D), a common floral associate in Eifelian gastropod-rich communities in various accreted Alaskan terranes (Farewell, Alexander, Livengood and Arctic Alaska).

ACKNOWLEDGEMENTS

Grateful appreciation is due Wyatt G. Gilbert, whose 1979 summer field mapping program in the McGrath A-4 and A-5 quadrangles, made possible the collection of the Cheeneetnuk Limestone specimens. Arlene V. Anderson kindly allowed examination of her doctoral dissertation collection from the Demarcation Point quadrangle, eastern Brooks Range of Alaska. RBB thanks the Alexander von Humboldt Stiftung for providing financial support that allowed him a six month stay in Germany to study European Devonian gastropods. AGC thanks Peter Jell and the Trustees of the Queensland Museum for support enabling travel to North America during 1997. We also wish to thank A.J. Boucot, Jiří Frýda, and Alex Nützel for their thoughtful reviews of this manuscript.

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